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Introduction

The Atlantic salmon is spawned in freshwater where it spends the first few years of its life. This freshwater phase can last as long as seven years (Mills, 1972) but in Scottish rivers is more usually two or three (Shearer, 1972). The salmon leaves the river as a smolt and spends at least one winter at sea where it maintains a very high rate of growth. During this period, the fish may also travel great distances. Fish spawned in Scottish rivers are found as far away as Norway (Harden Jones, 1968) and Greenland (Shearer, 1972). Although there is still some controversy concerning the homeward migration (Harden Jones, 1968), the weight of evidence suggests that fish return from these distant parts to spawn in the river of their birth (Stasko *et al.,* 1973b).

Our investigations have been concerned with that phase of the seaward journey of returning adults after they have encountered the Scottish coast, but have not yet begun their upstream migration. In this report, we describe in detail the movements of two salmon (fish returning after two or more winters at sea) and four grilse (fish returning after only one winter at sea) tracked during June and July 1979. A previous report describing preliminary studies carried out in 1978 has already been published (Hawkins *et al.,* 1979).

Methods

The study area

The fish were captured in bag nets at the Rockhall station of Messrs Joseph Johnston and Sons Ltd., some 8km north of Montrose on the east coast of Scotland. They were released approximately 0.5km offshore in at least 10m of water, and subsequently ranged up to 17km offshore and as far north and south as Aberdeen and the Bell Rock, respectively, before tracking was suspended. Tides in this area flow along a more or less north-south axis, flooding to the south and ebbing to the north. One tidal cycle is completed in approximately 13 hours. A more detailed description of the study area is given by Hawkins *et al.* (1979).

Tagging

Each experimental fish was caught in commercially fished bag nets, removed and immediately placed in a black polythene bag containing a solution of MS222 in sea water (1 part MS222 in 10,000). When deeply sedated, the animal was transferred to a wooden board where it was measured and a sample of scales removed for later age determination. A conventional hydrostatic tag was inserted immediately below the dorsal fin and an acoustic transmitter gently pushed into the stomach.

The fish was kept for between two and six hours in a cage on the sea bottom marked by a surface float. This period was to allow the fish to

recover from the stress of capture and its subsequent treatment with anaesthetic. The fish was later released from the cage by passing a messenger weight down the float line from the surface to release a catch holding the door closed. The fish was allowed to swim from the cage in its own time and was subsequently tracked by two boats provided with tracking equipment.

Tracking

The acoustic transmitters were supplied by the Fisheries Laboratory, Lowestoft, and emitted 1.5ms long pulses at a nominal 75 kHz once every 1.5 seconds. They were cylindrical in shape with a diameter of 14.7mm, and a length of 58mm, weighing some 23g in air and approximately 10g in water. The tag was completely encapsulated in epoxy resin (MMM Scotchcast) except for the switch terminals which were sealed by a cap of dental wax.

The transmitter was tracked by means of a Lawson Instruments model B ultrasonic receiver, with a directional hydrophone, operated from an inflatable boat powered by a 25hp (18.6 kW) outboard engine. The inflatable boat kept station with the tagged fish while the second boat, a 27 foot (8.2m) launch, recorded the position of the inflatable boat, and thus of the fish, at intervals of fifteen minutes.

The position of the vessel was fixed by means of a Decca Trisponder radio-navigational aid housed in the launch. The device provided the distance of the vessel from two stations on the mainland, each to a precision of $\pm$3m. Thus, by solving the simultaneous equations for two circles, the position of the fish on an arbitrary fixed rectangular grid was calculated. The tracking grid could be related to the Ordnance Survey grid as the positions of both stations on the mainland were known relative to both grid systems.

Tidal flow was measured directly by means of the launch, the Decca Trisponder system and a series of drogues. The drogues were made from two aluminium alloy sheets each 50cm x 70cm set at right angles to one another to form a cross-vaned drogue (Vachon, 1978) and suspended from a 20cm diameter trawl float by lines varying in length from 1m to 15m.

During the 15 minute periods between position fixes on the fish, one or two drogues were dropped near its position and tracked from the launch. At these times the inflatable vessel maintained contact with the fish. Positions of the drogues at five minute intervals were determined by means of the Trisponder system. Tidal monitoring was carried out at least once every hour.

The tidal flow was generally measured at depths of 1, 3, 5 or 10m. Inspection of the results showed little difference in the speed or direction of water flow at different depths, this observation being supported by occasional measurements taken with a direct reading current meter. We had no direct indication of the depth at which the tracked fish swam, but a shallow angle for optimal detection of the tag signal, our own catches of salmon by drift net at the surface and observations reported by Stasko *et al.*, (1973b), suggest that returning salmon in the open sea swim close to the surface. Drogue movements at either 1m or 3m were therefore taken as the best measures of tidal flow as it affected the salmon.

Definitions and data analysis

Following the convention set out in Baker (1978), the track of the fish was defined as the movement of the fish relative to the ground, and was simply the succession of fish positions given by the tracking system.

A series of vectors, the track vectors, describing average speed and direction of fish movement between successive positions were calculated from the track. Tidal vectors were calculated as the average speed and direction of movement of the drogues, determined approximately once every hour. For times between each direct measurement of the tide the vector was estimated assuming linear changes in speed and direction between measured flows. The course vectors describe the movements of the fish relative to the water and were calculated by subtracting the appropriate tidal vector from each track vector. The course or heading of the fish is thus the direction in which the fish attempted to swim with the deflecting effects of the tide removed.

During the major part of each tidal phase the speed and direction of tidal flow remained relatively constant. Thus linear interpolation between current measurements taken approximately one hour apart was a good estimator of tidal flow. Around periods of slack water, however, tidal speed and direction changed much more rapidly and to a far greater extent. Our sampling thus gave a less clear picture of tidal movements over periods of slack water. As the fish course vectors were calculated from both fish track and tidal vectors, they were thus especially open to error during periods of slack water. For this reason, such periods were removed from the data for some of the subsequent analyses by defining each tidal phase as occurring between a period one hour after the estimated time of slack water and one hour before the estimated time of the next slack water.

Results

Of the two salmon and four grilse tracked in 1979, none were observed entering rivers and only rarely were the fish tracked close inshore. Our comments on their movements are thus mostly restricted to behaviour in open water relatively distant from land and free from the effects of freshwater. Table I gives details of the six fish tracked and a brief description of their movements.

Table I

Details of the fish released and tracked in 1979. The age of the fish is expressed in terms of the number of years spent in freshwater followed by the number of years spent in the sea. All times are given as BST.

Fish	Released (Date and time)	Observations
Trident 74cm Salmon age 2.2+ years	20 Jun. 79 14.10	Moved rapidly offshore to E during the ebb tide, slowing and changing direction to ESE at low slack water. Tracking abandoned at 19.46.
Thor 85cm Salmon age 2.2+ years	26 Jun. 79 13.37	Moved S with flood tide, later altering track to SE. At high slack water changed direction to ENE, continuing in this direction during ebb tide until low slack water when the track reverted to SE during the succeeding flood tide. Tracking abandoned at 01.10 on 27 Jun.
Tempest 63cm Grilse age 3.1+ years	02 Jul. 79 22.35	Moved offshore and SE during the ebb tide, slowing and swinging E at low slack water before moving rapidly S on the flood tide. Slowed at high slack water, then moved NE on the ebb. At 16.00, and low slack water, changed track to the W meeting the coast at the North end of Lunan Bay. The fish crossed the bay with the flood tide, crossing the mouth of Lunan water. Continued S to Ethie Haven on the South shore of Lunan Bay at 20.30. Stayed close to the shore, moving back and forth close to the rocks. Still there at 22.30 when tracking was abandoned.
Trevor 64cm Grilse age 3.1+ years	05 Jul. 79 10.30	Moved NE against the flood tide altering course to SE at high water slack and then swinging to ESE against the ebb tide. At low slack water altered track to S, moving rapidly with the flood tide to pass the mouth of the river South Esk. Off Scurdie Ness the fish altered track towards offshore, and ESE, slowing at slack water, when tracking was abandoned.
Tristan 62cm Grilse age 3.1+ years	09 Jul. 79 16.41	Moved SE during the ebb tide, altering track to S at low slack water and then moving very rapidly S with the flood tide. Passed to the east of the Bell Rock lighthouse off the Tay estuary at 03.30 on 10 July still moving rapidly with the flood tide. Tracking abandoned at 04.32 on 10 July.
Tennyson 66cm Grilse age 3.1+ years	16 Jul. 79 16.09	Moved S with the flood tide, slowing at high water slack and altering track to move rapidly NE on the ebb tide. Slowed at low slack water, reversing to move slowly SW during flood tide. Reversed track again at high slack water moving rapidly to the NE again, on the ebb tide. Tracking abandoned with the fish approximately 10km to the east of Johnshaven.

Orientation

Figure 1 shows the track and calculated course of each fish tracked over at least one tidal phase. The courses were calculated by assuming an arbitrary starting point and then calculating successive positions using, in turn, each course vector and the time during which the fish remained on that vector.

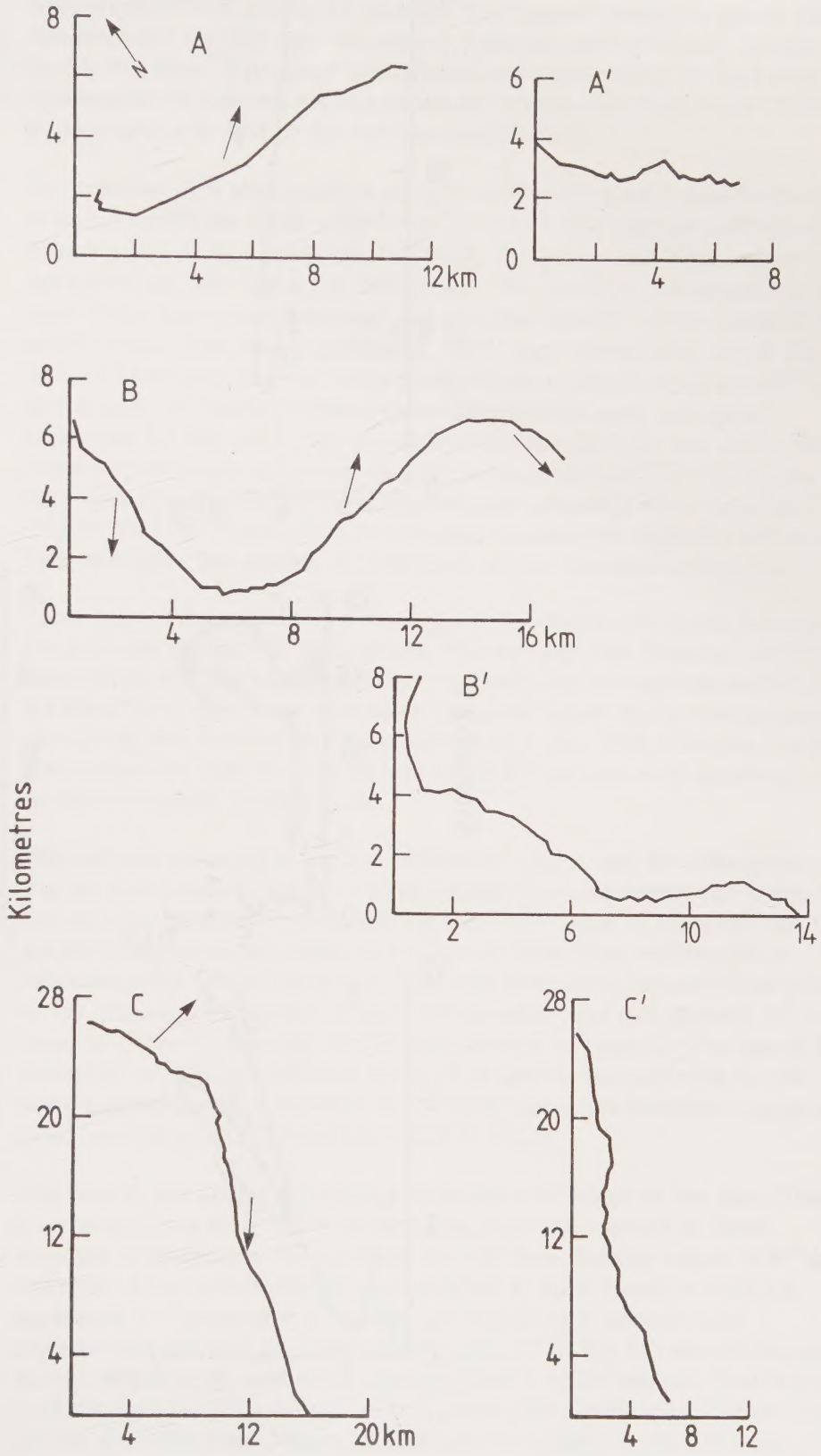


Figure 1. The offshore movements of Atlantic Salmon. For each fish, the left hand map shows the track, with the direction but not speed of the tide indicated by arrows for each tidal phase. Right hand maps (letters dashed) show fish course where tidal vectors have been subtracted. North in all maps is as indicated on map A.

Individual fish are A: Trident, B: Thor, C: Tristan, D: Tempest, E: Trevor, F: Tennyson.

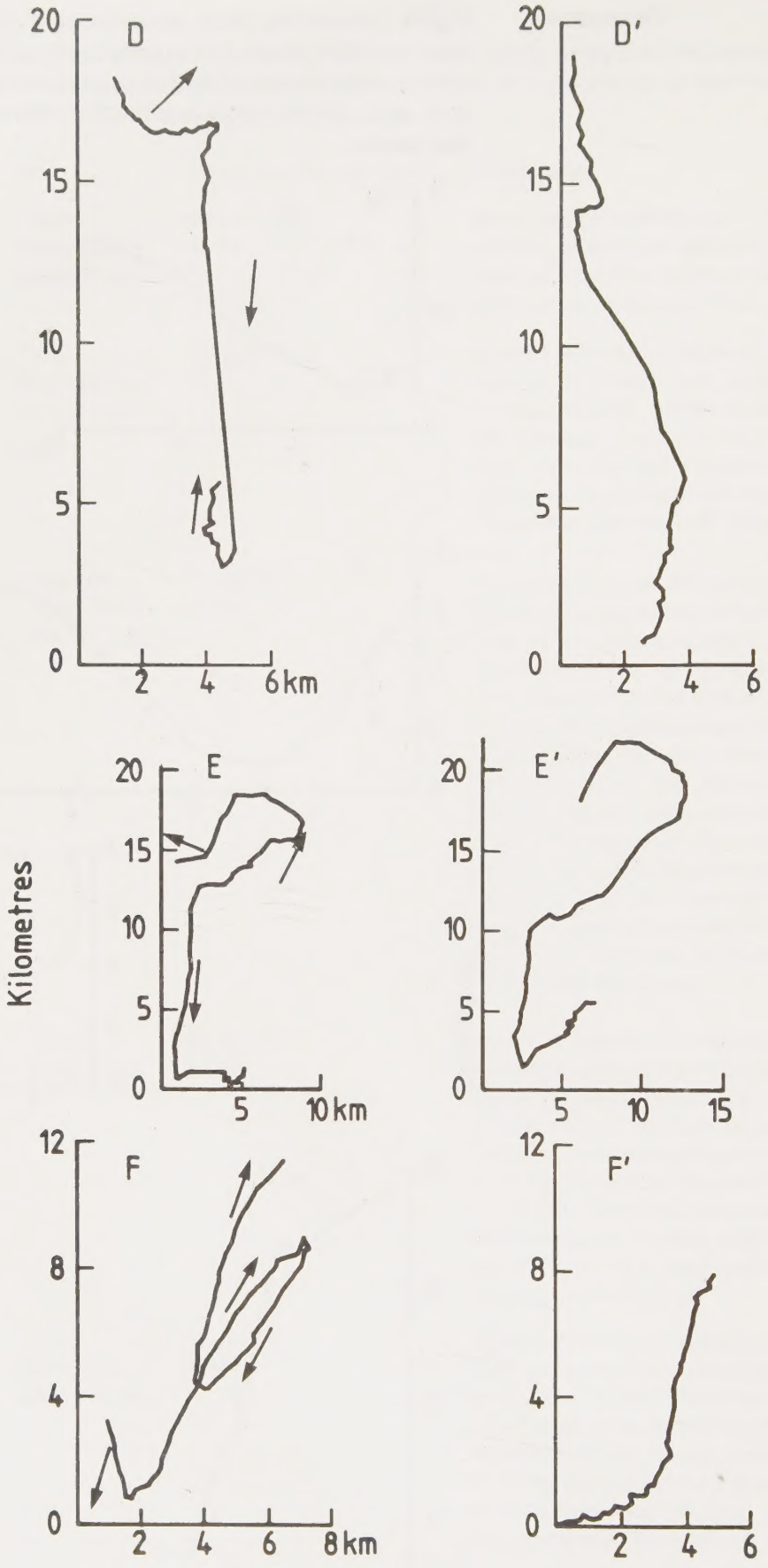


Figure 1. The offshore movements of Atlantic Salmon. For each fish, the left hand map shows the track with the direction but not speed of the tide indicated by arrows for each tidal phase. Right hand maps (letters dashed) show fish course where tidal vectors have been subtracted. North in all maps is as indicated on map A.

Individual fish are A: Trident, B: Thor, C: Tristan, D: Tempest, E: Trevor, F: Tennyson.

Complex patterns of movement were shown in the tracks of fish over the ground, the tracks clearly being influenced by the tidal currents. The complexity essentially disappeared with calculation of the swimming course, where the deflecting influence of the tide was removed. Thus, the fish designated 'Tennyson' (Fig 1f) maintained an approximately straight line course of ENE during 21 hours of tracking and three changes of tide. Movement of the fish over the ground, however, was extremely complex during this time. 'Tennyson' was subsequently recaptured six days after termination of the tracking in a sweep net on the river Spey some 200km by sea north and west of the last recorded position.

The tracking data also provided an opportunity for a more quantitative examination of the fishes' orientation. For each fish tracked over more than one full phase of the tide, fish track, fish course and tidal vectors were grouped with respect to tidal phase. The distances corresponding to each vector were then calculated and grouped into 20^{o} sectors according to vector angle. Rose diagrams (Mardia, 1972) were produced in which the radius of each segment was made proportional to the distance moved within each 20^{o} sector. These angular distributions were calculated separately for fish track, fish course and tide for each fish and each tidal phase and corrected to correspond to a constant duration of four hours for each tidal phase to ease comparisons between phases of differing length (Fig 2). The fish 'Trevor' (Fig 1e) showed qualitatively different behaviour from the other fish studied in 1979, and will be discussed separately.

Table II gives the statistics for the angular distribution of course for each fish summed through all tidal phases. The Rayleigh test (Mardia, 1972) was used to test the null hypothesis that no directional preferences existed in the data. Such movement relative to the water shows strong and consistent directional bias through all tidal phases in each fish. This is despite the fact that movement over the ground is in each case complex and apparently greatly influenced by tidal flow.

The uniform scores test (Mardia, 1972) was used to test for differences in angular distributions. Table III gives the results of comparing fish track distributions between tidal phases for each fish. Table IV gives the results of the same test on distributions of fish course. Significant differences in fish movement relative both to ground and water exist between tidal phases for all fish except 'Tristan'. In each case however, the test statistic, R*, is lower in Table IV than the corresponding value in Table III. Changes in the direction of salmon movement can thus be seen to be magnified by the deflecting influence of the tidal flow whose speed and direction change with time, confirming the feature illustrated in Figure 1.

Fish course also changed gradually from one tidal phase to the next. There is some evidence from Table IV, however, that this was not in direct response to changes in the direction of tidal flow. Smaller values of R* do not occur when distributions corresponding to both floods or ebbs are compared. In fact smaller R* values are associated in general with comparisons between successive tidal phases. Thus the fish course changed slowly with time in response to some influence which was not tidal in origin. Such changes are large enough to show statistical significance, but are much smaller than the direct effects of tidal deflection seen in the fish tracks.

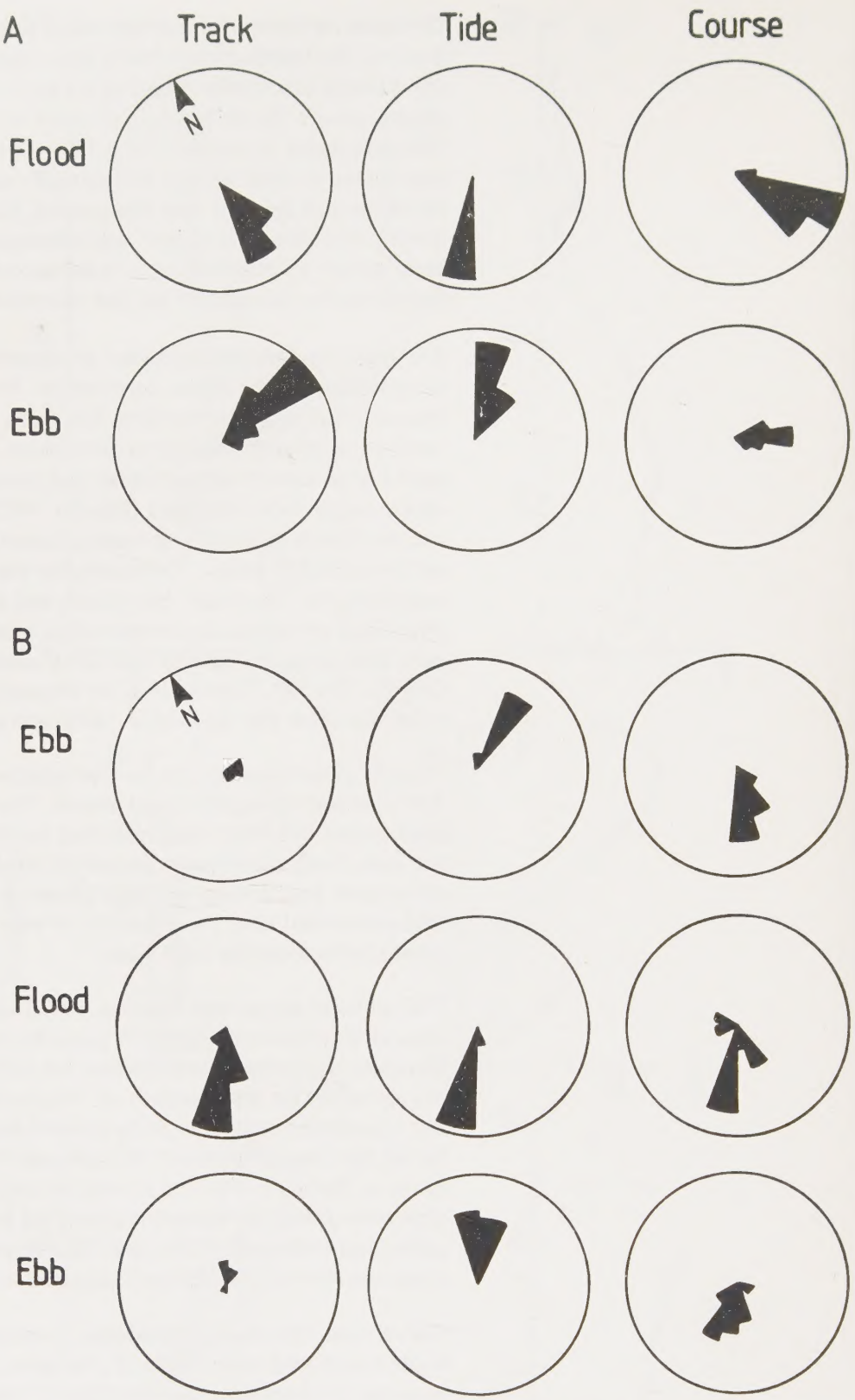
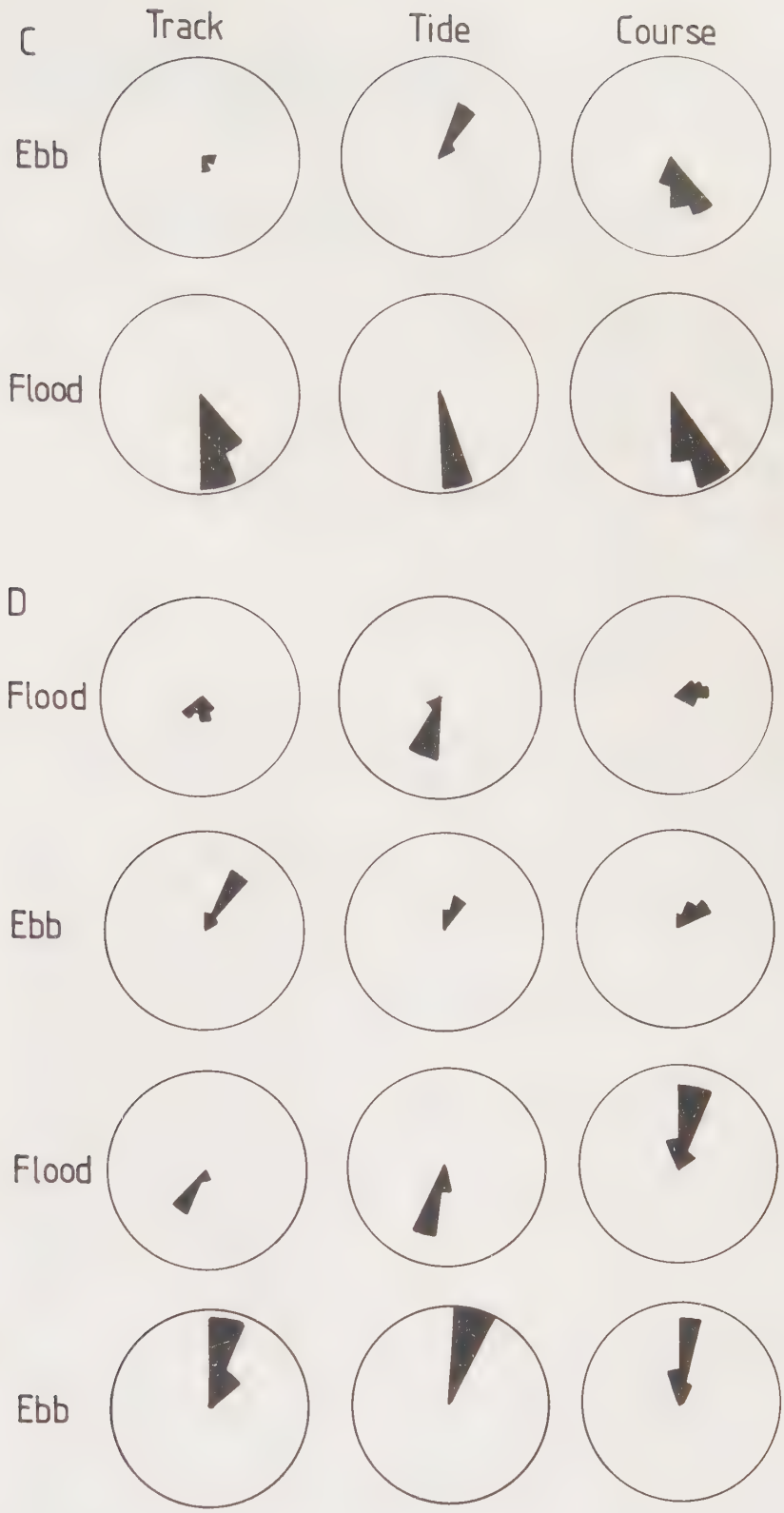


Figure 2. Angular distributions of fish track, course and tide for each fish and tidal phase separately. In each rose diagram, the length of the radius of each 20° sector is proportional to the distance moved in that direction, corrected to a constant observation time of 4 hours. The distances, in kilometres, corresponding to the radii of the circles are:—

	Track	Tide	Course
A: Thor	5	5	4
B: Tempest	5	4	2
C: Tristan	12	9	8
D: Tennyson	7	8	3



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	Track	Tide	Course
A: Thor	5	5	4
B: Tempest	5	4	2
C: Tristan	12	9	8
D: Tennyson	7	8	3

Table II

Statistics for the angular distributions of course for each fish summed over the whole tracking period. Rayleigh test of circular uniformity (Mardia, 1972), critical value for $p = 0.001$, $2n\bar{R}^2 = 13.82$

Fish	Mean Direction (Compass Degrees	Circular Standard Deviation (Degrees)	Rayleigh Test $2n\bar{R}^2$	Significance Level
Trident	126.2 (SE)	24.7	529.6	$p<0.001$
Thor	133.4 (SE)	25.1	990.3	$p<0.001$
Tempest	205.8 (SSW)	35.2	1173.2	$p<0.001$
Tristan	187.6 (S)	13.7	1093.9	$p<0.001$
Tennyson	61.0 (ENE)	44.2	723.4	$p<0.001$

Table III

Comparison of angular distribution of fish track between tidal phases for each fish tracked for more than one phase of the tide. Uniform scores test (Mardia, 1972), critical value of R* for $p = 0.001$, 13.82

Fish	Tidal Phases Under comparison	Uniform Scores Test R^*	Significance Level
Thor	Flood 1 v Ebb 1	124.65	$p<0.001$
Tempest	Ebb 1 v Flood 1	36.18	$p<0.001$
	Ebb 1 v Ebb 2	46.31	$p<0.001$
	Flood 1 v Ebb 2	42.83	$p<0.001$
Tristan	Ebb 1 v Flood 1	98.38	$p<0.001$
Tennyson	Flood 1 v Ebb 1	50.90	$p<0.001$
	Flood 1 v Flood 2	33.15	$p<0.001$
	Flood 1 v Ebb 2	47.19	$p<0.001$
	Ebb 1 v Flood 2	81.75	$p<0.001$
	Ebb 1 v Ebb 2	52.37	$p<0.001$
	Flood 2 v Ebb 2	90.87	$p<0.001$

Table IV

Comparison of angular distribution of fish course between tidal phases for each fish tracked for more than one phase of the tide. Uniform scores test (Mardia, 1972), critical value of R* for p = 0.05, 5.99

Fish	Tidal Phases Under Comparison	Uniform Scores Test R*	Significance Level
Thor	Flood 1 v Ebb 1	27.17	$p<0.001$
Tempest	Ebb 1 v Flood 1	6.44	$p<0.05$
	Ebb 1 v Ebb 2	29.80	$p<0.001$
	Flood 1 v Ebb 2	13.82	$p<0.01$
Tristan	Ebb 1 v Flood 1	2.96	NS
Tennyson	Flood 1 v Ebb 1	3.93	NS
	Flood 1 v Flood 2	30.47	$p<0.001$
	Flood 1 v Ebb 2	15.50	$p<0.01$
	Ebb 1 v Flood 2	23.00	$p<0.001$
	Ebb 1 v Ebb 2	11.82	$p<0.01$
	Flood 2 v Ebb 2	12.41	$p<0.01$

After the initial period of orientation immediately following release, one fish, 'Trevor', changed course markedly twice during tracking (Fig 1e). The turns occurred approximately half-way between high and low water slack and again half-way between low water and the next high water slack. In both cases, the fish turned to move upstream against the tide. As 'Trevor' was, on both occasions, close to the mouths of rivers and this behaviour would have taken him into areas of lower salinity, freshwater may have been a stimulus for the behaviour. 'Trevor' was the only fish to act in this way in 1979 though similar observations were made in 1978 for fish tracked close inshore.

In 1979, both 'Tristan' and 'Tempest' also passed river mouths at approximately the same distance as 'Trevor'. As they were released at a different phase of the tidal cycle and as we could not measure salinity at the exact fish positions, we cannot say whether these fish ignored or simply did not detect the river outflows.

Swimming speed and energetic efficiency

For each fish tracked in 1979, fish length was converted to weight using a weight/length relationship calculated specifically from fish caught in the Montrose area during the months of June and July. Data from Brett (1965) on the swimming performance of sockeye salmon (*Oncorhynchus nerka*) were then used to calculate the energy costs of moving a constant distance of 1 km at a series of different swimming speeds. Figure 3 gives an example of such a curve. In fact, the curves for the fish tracked are very similar. Minimum energy consumption ranged from 49.6 to 67.4 mg 0_2 $kg^{-1}km^{-1}$ with larger fish incurring lower relative costs. These minima occurred at speeds from 0.51 to 0.59 body lengths per second, larger fish reaching their minima at lower relative speeds.

For the fish tracked, the mean speed of movement through the water was calculated separately for each tidal phase. The data are given in Table V, the observed swimming speeds being indicated on the cost curve in Figure 3.

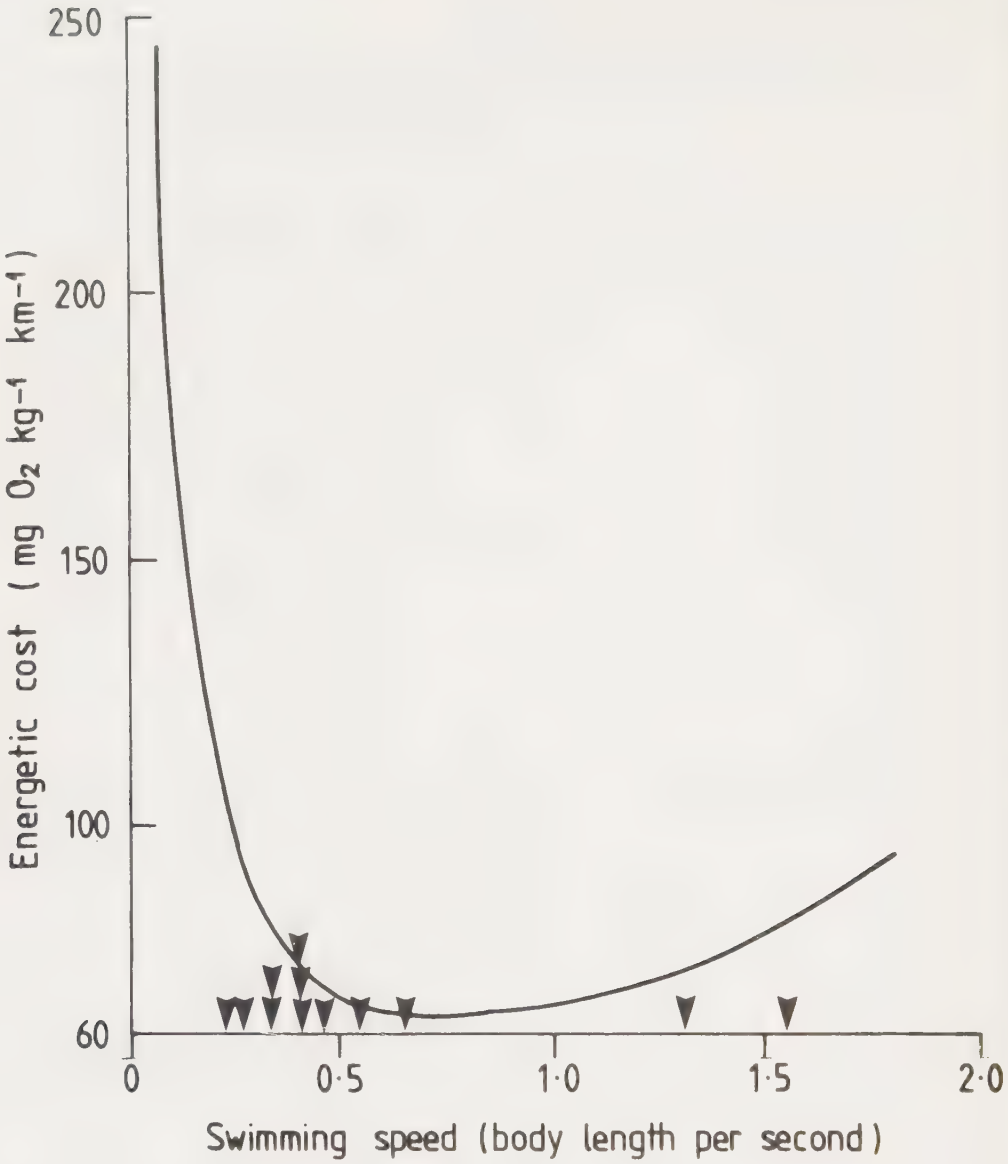

Figure 3. The energetic costs of swimming. The curve is representative of the energetic costs of swimming at different speeds for the fish described in this study. The limits within which such curves fall for the actual fish tracked are given in the text. The arrows indicate average swimming speeds relative to the water calculated separately for each fish and tidal phase described in this study (see Table V).

If we define the most efficient swimming speed as that which provides the lowest energetic cost per unit distance travelled, then all the fish except one swam either very close to or under their most efficient speed. The remaining fish, 'Tristan', swam at approximately three times the calculated most efficient speed. However, this fast swimming speed resulted in an increase in cost per unit distance of only 19%, due to the shallow slope of the curve above the most efficient speed. 'Tennyson', on the other hand, moving at just under half the most efficient swimming speed incurred an increased cost of approximately 64% over the calculated minimum.

Table V

Speed, and the energetic cost of movement through the water, for Atlantic salmon tracked in 1979

Fish	Tidal Phase	*Speed through the water (Body Lengths per second)		*Cost of movement (mg 0_2 kg^{-1} km^{-1})		% Increase of Cost over Minimum
		(a)	(b)	(a)	(b)	
Trident	Ebb	0.54	0.54	56.59	56.59	0.0
Thor	Flood	0.65	0.51	50.91	49.59	2.7
	Ebb	0.46	0.51	51.51	49.59	3.9
Tempest	Ebb	0.35	0.59	83.49	66.12	26.3
	Flood	0.41	0.59	77.49	66.12	17.2
	Ebb	0.36	0.59	84.48	66.12	27.8
Tristan	Ebb	1.31	0.59	74.37	67.39	10.4
	Flood	1.55	0.59	80.51	67.39	19.5
Tennyson	Flood	0.41	0.57	73.96	63.44	16.6
	Ebb	0.24	0.57	103.78	63.44	63.6
	Flood	0.42	0.57	73.87	63.44	16.4
	Ebb	0.27	0.57	92.52	63.44	45.8

*(a) Speed and energetic costs for fish tracked in 1979

(b) Speed and energetic costs at calculated most efficient swimming speeds

Energy partitioning for each fish at its most efficient swimming speed, calculated as above, was investigated as follows. The resting metabolic rate and total costs of movement, measured in terms of 0_2 consumption, were both calculated from empirically derived formulae for sockeye salmon given by Brett (1965). Subtracting resting metabolic costs from total costs of swimming gave the costs of locomotion on the assumptions that maintenance costs do not change with swimming speed, and that no other energetic costs are involved in locomotion. The results of the calculations are given in Table VI. At the most efficient speeds, each fish would partition energy almost equally between the costs of propulsion and resting metabolism. The data agree well with the conclusions of Weihs (1973) who made predictions of energy partitioning largely from theoretical considerations of the dynamics of fish swimming.

Swimming speeds and tidal flow

For each fish tracked over at least one tidal phase, swimming speed through the water was plotted against measured tidal speeds over all tidal phases and regression equations determined. The data for periods of slack water were discarded for the reasons discussed above. The results are given in Table VII and show no clear pattern. The only significant correlation has a positive gradient. Of the other four fish, two showed positive relationships while the other two were negative.

Tidal flow has direction as well as speed, however, and the relative angle between tidal flow and fish movement through the water may be an important factor in modulating fish swimming speed. To keep this relative angle constant, the regressions were recalculated for each fish and tidal phase separately. As can be seen from Figure 2, the direction of fish course and tidal flow are relatively consistent within tidal phases.

Table VI

Energy partitioning between costs of movement and resting metabolism at maximally efficient swimming speeds through the water

Fish	Most Efficient Swimming Speed (Body Lengths per second)	*Resting Metabolic Rate (mg O_2 kg^{-1} h^{-1})	*Cost of Propulsion (mg O_2 $kg^{-1}h^{-1}$)
Trident	0.54	35.03 (43)	46.65 (57)
Thor	0.51	31.63 (41)	46.09 (59)
Tempest	0.59	38.66 (44)	49.39 (56)
Tristan	0.59	39.08 (44)	49.22 (56)
Tennyson	0.57	37.47 (44)	49.08 (56)

*Figures in brackets refer to the percentage of total rate of energy consumption at maximally efficient swimming speeds

Table VII

Results of the regression of fish swimming speed through the water against rate of tidal flow over all tidal phases; both speeds were expressed in cm s^{-1}

Fish	Regression Coefficient	Y Intercept	F (df)	Significance Level
Trident	—0.69	78.1	1.58 (1,15)	NS
Thor	—0.16	48.0	0.18 (1,20)	NS
Tempest	0.59	11.8	2.51 (1,33)	NS
Tristan	0.77	37.4	5.92 (1,32)	$p < 0.025$
Tennyson	0.88	15.3	0.56 (1,31)	NS

The results of the regressions are given in Table VIII. Of the 12 regressions calculated, only three provided significant relationships between tide and swimming and all of these had positive regression coefficients. Only two of the twelve regression coefficients were negative.

Periodicity in swimming speeds

Table IX gives the maximum calculated swimming speeds relative to the water for the fish analysed above. Each value is an average speed calculated from fixes taken at least 14 minutes apart. To obtain information for the whole 24-hour period, the data for all fish were combined. To reduce biases from fish that swam consistently faster than others, the swimming speeds of all fish were corrected to a scale of 0 to 100 where 100 corresponded to the maximum calculated swimming speed of that fish.

Table VIII

Results of regression of fish swimming speed through the water against rate of tidal flow for each fish and tidal phase separately; both speeds were expressed in cm s^{-1}

Fish	Tidal Phase	Regression Coefficient	Y Intercept	F (df)	Significance Level
Trident	Ebb	− 0.69	78.1	1.58 (1,15)	NS
Thor	Flood	0.01	51.1	0.0003(1,4)	NS
	Ebb	0.38	21.3	0.96 (1,14)	NS
Tempest	Ebb	1.09	− 2.9	15.55 (1,12)	$p<0.0025$
	Flood	2.65	− 24.9	2.48 (1,8)	NS
	Ebb	0.06	20.48	0.03 (1,17)	NS
Tristan	Ebb	0.77	39.7	2.09 (1,16)	NS
	Flood	0.74	36.7	6.17 (1,14)	$p<0.05$
Tennyson	Flood	0.20	17.5	0.77 (1,7)	NS
	Ebb	0.14	9.9	0.33 (1,10)	NS
	Flood	− 0.04	23.9	0.02 (1,3)	NS
	Ebb	0.27	1.5	6.86 (1,5)	$p<0.05$

Table IX

Maximum calculated swimming speeds through the water

Fish	Maximum calculated Speed through the water (cm s^{-1})
Trident	87
Thor	78
Tempest	89
Tristan	176
Tennyson	68

The diurnal periodicity of activity was investigated in each fish separately using the average corrected speed through the water during each half hour of tracking. Figure 4a shows the activity patterns of all fish plotted on the same graph. The graphs for each fish show broad similarities in the times of major activity peaks and minima, thus justifying combination of all data to give a composite view of their activity through the day (Fig 4b). This shows a pronounced peak in the early morning. Sunrise during the period of tracking was between 03:10 and 03:30 G.M.T. (HMSO, 1977). Minimum activity occurred around mid-day and was followed by generally higher activity later in the afternoon. Swimming speed fell to an intermediate level during the hours of darkness.

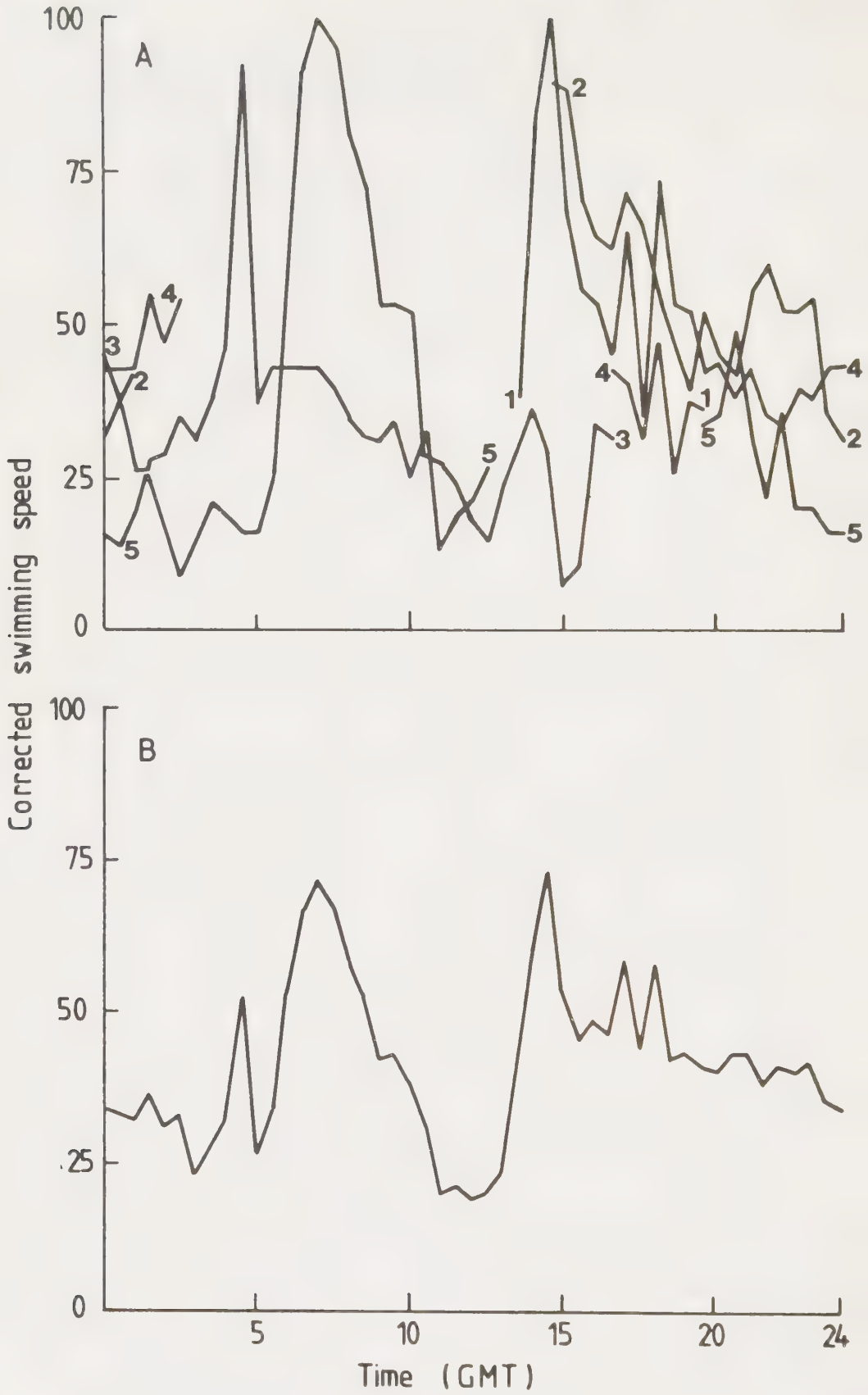

Figure 4. Swimming speeds relative to the water and time of day.

A shows the activity patterns of five fish plotted individually. The fish are 1: Trident, 2: Thor, 3: Tempest, 4: Tristan, 5: Tennyson.

B shows the general pattern of salmon activity, where the swimming speeds of the same fish as in A have been averaged together in periods of half an hour throughout the day.

Discussion

Orientation

The tracks of the migrating salmon observed in this study were very complex and showed little consistency of pattern between individual fish. This feature, illustrated in Figure 1, has been encountered by many other workers in the field of fish migration including Madison *et al.* (1972), Stasko (1975) and Stasko *et al.* (1973a). The present study showed, however, that subtraction of tidal flow from such movements produces a set of swimming courses giving a clearer indication of the salmon's ability to set and maintain a course. In this study, all fish save one maintained a much more constant swimming course than would have been indicated by the track. The complexity of the track was caused by the deflecting influence of the tide which changed its speed and direction of flow periodically.

For four out of five of the fish tracked in open water, however, swimming course did change over time (Table IV) although the changes did not appear to be related to changes in the direction of tidal flow. One explanation for the variation is that salmon may be unable to maintain a precise course over long periods of time. Another is that the changes are a response to changing relative positions of the salmon and its final destination, caused for example by tidal deflection. This latter explanation demands that the fish have fairly precise information on the relative position of that final destination. At present we cannot reject either of these hypotheses, nor can we suggest a sensory mechanism to account for the maintained orientation.

De Veen (1978) and Greer Walker *et al.* (1978) have shown that some species of flatfish move in a fashion termed selective tidal stream transport. With this behaviour, the fish uses favourable tides to maximise its speed of movement over the ground. When the direction of the tide changes, however, the fish moves to the sea bed and 'sits out' the unfavourable flow. Weihs (1978) has shown that such a strategy is very efficient in terms of the energy costs of moving from one place to another.

It is evident from our work that salmon do not employ such an extreme strategem. They certainly do not cease swimming and seek the shelter of the bottom during unfavourable tides. The fish 'Tennyson' (Fig 1f), for example, lost ground through swimming against a relatively strong, unfavourable tide. We have no data on the depths at which the salmon swam during tracking, however, and we therefore cannot, at this stage, discount the possibility that salmon migrate vertically during the homeward migration to take advantage of any favourable changes in the direction of tide with depth.

Swimming speed and energetic efficiency

Of the fish tracked in 1979, all except one swam very close to or below its most efficient swimming speed, defined as the speed at which least energy is consumed per unit distance travelled. The fish would therefore appear to be minimising the energetic costs of their sea journey to the river mouth at the expense of the time taken. The shape of the energy cost curve (Fig. 3), however, shows that swimming at speeds greater than the most efficient is proportionately less expensive than swimming below it. Slower speeds must therefore have advantages other than the direct saving of energy, for example allowing the possibility of feeding en route or being necessary for navigation. It is interesting to note also that the speeds taken up by the majority of the fish correspond to minimising energy costs per unit time, given the underlying constraint of keeping costs per unit distance low. We cannot entirely rule out the effects of the tag in slowing the fish to a speed lower than is usual. However, data from Atlantic salmon marked with conventional numbered tags and subsequently recaptured give speeds over the ground of 19 to 29 cm s^{-1} (Went, 1973), values which agree very well

with the data from our present study. The distance of the fish from its home river as well as size and physiological condition may also have effects which would explain some of the variability in swimming speeds observed in different fish.

The cost curve as presented in Figure 3 thus provides only an indication of the speed at which migrating salmon should swim. As well as those factors discussed above, the effects of tide may affect the most advantageous swimming speed for returning fish. A model which takes account of the effects of tide on the energetics of swimming speeds is discussed below.

Swimming speed and tidal flow

From Table VIII, there appears to be a positive relationship between the salmon swimming speed relative to the water and the speed of tidal flow. This finding is in agreement with observations made on American shad (*Alosa sapidissima*) by Dodson and Leggett (1973). Of the three relationships found to be statistically significant, two, for the fish 'Tennyson' and 'Tristan', were found when the tide opposed fish course; the other, for the fish 'Tempest', occurred when the tide flowed in the same direction as fish course. Dodson and Leggett (1973) reported that migrating shad generally exhibited counter current orientation during both ebb and flood tides, and this was clearly not the case with the salmon in this study.

Leggett and Trump (1977) and Trump and Leggett (1980) have investigated, using mathematical models, the relative energetic costs of different behavioural responses to currents. Their work suggests that the most energetically efficient swimming strategem in an environment where tidal flow varies is to swim at a constant speed relative to the mean tidal velocity, ignoring periodic variations in that velocity.

From Trump and Leggett (1980) the optimum speed is given by

$$W_0 = U_0 + {}^1/_b \quad \ldots\ldots\ldots\

Table X

Tidal velocity and most energetically efficient swimming speeds

Fish	Mean tidal velocity ($cm\ s^{-1}$)	Mean swimming speed through water ($cm\ s^{-1}$)	*Expected swimming speed ($cm\ s^{-1}$)
Trident	49.6	40.2	177.8
Thor	32.2	55.6	167.3
	46.3	39.1	181.4
Tempest	23.6	22.4	145.6
	30.2	26.1	152.2
	35.1	22.6	157.1
Tristan	51.8	81.3	172.3
	59.5	96.2	180.0
Tennyson	36.4	26.7	158.4
	28.1	14.2	150.1
	56.1	29.3	178.1
	55.1	18.1	177.1

*calculated from equation (1) and the 'b' values calculated from Brett (1965).

Table XI

Tidal velocity and most energetically efficient swimming speeds, all tidal phases combined

Fish	Mean tidal velocity ($cm\ s^{-1}$)	Mean swimming speed through water ($cm\ s^{-1}$)	*Expected swimming speed ($cm\ s^{-1}$)
Thor	7.18	47.37	142.3
Tempest	3.29	23.67	125.24
Tristan	20.54	88.76	141.02
Tennyson	13.84	20.16	135.79

*calculated from equation (1) and the 'b' values calculated from Brett (1965).

Even if the model truly reflected the salmon's response to the tide, a major problem involved in fitting it to real data is in deciding the period over which the tidal speed should be integrated to coincide with the behaviour of the animal. The size of the disparity between salmon swimming speeds and those predicted by the model suggests, however, that even taking this difficulty into account the model does not adequately describe the behaviour of these migrating salmon.

Trump and Leggett (1980) further suggest that fish may be unable to respond to tidal speeds averaged over a period of time, but may react to the tide by correcting speed according to equation (1) as a result of more or less instantaneously perceived tidal velocities. If behaviour of the salmon described in this report fitted such a model, the regressions in Table VIII would be expected to have a slope of 1 and an intercept on the y axis of between 120 and 135 ($^1/_b$). The three significant regressions were tested and all showed significant differences between predicted values and the regression equations. ('Tempest', slope t = 0.316, 'Tristan', slope t = 1.193.

For both, however, the y intercept was outwith 95% confidence limits of the predicted y value when x was set to zero.) For 'Tennyson' the slope was significantly different from 1 ($t = 7.257$, $df = 5$; $p<0.001$). Thus, there is no evidence to suggest that migrating salmon behave in a way which minimises energy consumption in the manner suggested by Trump and Leggett (1980). One explanation is that all factors affecting maximally efficient swimming speeds have not been incorporated into the model, for example the restriction in the model that direction of salmon swimming must be on the same axis as that of tidal flow. Another is that salmon may be unable to determine tidal velocities in the open sea. Finally, it is possible that energy saving is not the most important consideration in determining swimming strategy at this stage in the migration.

Diel periodicity in swimming speeds

Madison *et al.* (1972) noted that returning sockeye salmon in the coastal waters of British Columbia showed pronounced diurnal periodicity in their swimming speeds. Highest swimming speeds occurred in the early afternoon and the lowest at about midnight. Johnson (1960) also reported a diurnal periodicity in the swimming activity of chinook salmon (*Oncorhynchus tshawytscha,* Walbaum) in a river system. Again little or no activity was recorded at night. Dodson and Leggett (1973), on the other hand, found no evidence of such diurnal rhythms in the swimming speed of American shad in coastal waters and, similarly, Stasko (1975) found no diurnal periodicity in the activity of Atlantic salmon in estuarine waters. From Figure 4, though there is evidence of a diel periodicity in the swimming speeds of salmon tracked in this study, the pattern shown is quite different to that reported by Madison *et al.,* (1972) and Johnson (1960), and swimming speed is at its minimum in the early afternoon. Further, the peaks in mid and late afternoon may be explained as artefacts. All of the fish were released during these times and the peaks may thus merely reflect increased activity soon after disturbance. Thus, it is possible that only the peak in the early morning truly reflects the activity pattern in the migrating salmon.

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Summary

Four grilse and two salmon were caught in bag nets at a coastal netting station, tagged with acoustic transmitters and subsequently tracked for periods ranging from 5 to 21 hours. During the tracking, tidal flow was also measured directly. Fish which swam offshore maintained a relatively constant heading independent of the speed and direction of the tide. One fish, which appeared to be affected by freshwater from river outflow, twice changed course to swim upstream against the tide. Swimming speeds in the fish were close to those expected if the fish were minimising energy expenditure per unit distance travelled.

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